A STUDY OF AMERICAN PETRIFIED CALAMITES¹

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The only extensive account of American petrified calamites is that by Andrews (1952), based on a portion of the collection of calamites in his laboratory. Since that time a large number of specimens has been added to this collection which forms the basis for the present investigation. From a study of these it has been possible to determine significant criteria for evaluating species of stem fragments, to record European species as present in American coal balls, and to give definite statistics for established American species. A number of stems fall into two new species, and one fragment is apparently new but too poorly preserved to receive specific assignment. Roots are numerous, and two new species are described. A few coal balls contain an abundance of leaves of a new species of cone, the first calamitean cone to be described from American coal balls. Finally, a stratigraphic and geographic tabulation is presented based on material within the scope of this investigation.

STEMS

Most of the work on petrified stems has been done by Williamson, Renault and Knoell. Williamson (1871, 1871a, 1878, 1883; Williamson and Scott, 1895, 1895a) described calamites and other fossil plant groups almost strictly from a morphological and anatomical viewpoint. He was loath to found species upon fragments of plants but was not unaware that some variation in stems was specific, and in one instance he did itemize variations of primary rays. Most of the taxonomic work was done by Renault (1885, 1886, 1895-1898) who used a variety of characters to distinguish species. Some characters are sound, such as pitting in tracheids, variation in primary and secondary rays, and orientation of primary tissues; but others, such as internode length based on one small fragment, regularity and frequency of branching, and pith and stem diameter, have proved to be unreliable. Also, varieties of Arthropitys bistriata (Cotta) Goeppert were formed on differences that would appear to be clearly specific. Knoell (1935) described some new species and varieties of stems but did not correlate them with previously described species. The use of characters observed chiefly from cross-sectional views is an additional confusing aspect of her work. Arthropitys communis was split into two entities, the species and a variety, based upon difference in the manner of primary ray diminution. The species was more closely defined and therefore designated as a new combination, Arthropitys communis (Binney) Hirmer & Knoell.

This new combination is not valid and the correct name should be Arthropitys communis (Binney) Renault.

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It is apparent from the literature that taxonomy of calamitean stems is inconsistent, and unreliable criteria have sometimes been used to separate species. For purposes of clarification the following is a suggested evaluation of stem characters offered as a guide to the delimitation of species.

I. Stem Diameter.—As a distinguishing character this is probably totally unreliable. Only Arthropitys gigas (Brongniart) Renault is partially distinct because of its large size.

II. Internode Length.—From a study of impression calamites the wide range of internode lengths in one specimen is immediately apparent. In petrified stems it

is best to avoid using this feature unless it is constant in several specimens.

III. Branching.—This is a major feature in classifying impression calamites. However, unless a petrifaction is so well preserved that its branching can be correlated with impression types, it has little diagnostic value.

IV. Pith.—Whether or not pith is preserved at the periphery and as nodal discs is a matter of age of the stem or fossilization conditions. Pith is the same in all calamitean stems: large, unordered, thin-walled parenchyma. Sometimes dark-colored cells are seen singly or in groups and are of diagnostic value and called resinous cells by some paleobotanists.

V. Primary Wood.-Primary wood of each pole is of small amount and borders the protoxylem canal on the outer side. Written description does not serve well to characterize primary wood. Orientation of pith cells about the pole, orientation of tracheids about the protoxylem canal, and relationships with secondary woodall form a picture varying in each species, and unless illustrated they are of little diagnostic value. Caution is necessary in using the size of the protoxylem canal, for it varies with pith diameter somewhat. This also holds true for the distance between protoxylem poles and width of the fascicular segment. The problem of whether primary wood of the Calamitaceae had endarch or mesarch development has never been resolved, although most authors believe in endarch development for the family. Andrews (1952) described a specimen from Mineral, Kansas, that has a relatively large amount of small, thick-walled cells surrounding the protoxylem canal, giving the appearance of mesarch development. Appropriate radial sections showed no pitting on the cells centripetal to the canal, but this is no disproof of centripetal xylem since preservation is far from good. Despite subsequent collection of a large number of stems from the Kansas locality, none of them are of his "species A" type.

VI. Fascicular Segment.—This structure, as a whole, is somewhat stereotyped although its width near the primary wood and rate of widening are specific. Sometimes the segment loses its identity in outer wood due to loss of the primary ray. Tracheid size is constant and of no diagnostic value. Pitting, however, is a fundamental character and is the principal reason for making radial sections of wood. In most calamites the primary tracheids are annular and scalariform, while secondary tracheids may be scalariform, reticulate, or pitted. Usually calamites have one type of pitting in secondary wood or a quick change from scalariform to pitted near the

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pith; but rarely a scattered mixture of the three types occurs in one stem. Previous authors have expressed doubt about the diagnostic value of pitting because of this occasional mixture of pitting types and the fact that the interface between tracheids and secondary ray cells is covered with scattered simple pits. Such detail is usually blurred in petrified calamitean stems, and it is difficult to tell simple pits from bordered pits. In any radial section there are likely to be tracheid walls exposed that lie against ray cells. Areas of simple pits so exposed may be found on a tracheid of Arthropitys communis known to have scalariform tracheids only. An area free of ray cells should be selected for study of pitting to avoid this difficulty. Secondary rays may be specific because of their relative frequency, the length of cells, and whether they are simple or compound. Increased frequency and multiseriate conditions in outer wood occur in the same stem; hence, tangential sections from inner wood and outer wood should be made to obtain a true picture of ray conditions. Radial sections show better the height of ray cells. VII. Interfascicular Segment or Primary Ray.-Although synonymy of these two terms is here implied, the primary ray carries a more restricted meaning; in calamite literature it is that part of the interfascicular segment made up of parenchyma.

The interfascicular segment is the most variable tissue in calamite steles and is used as a fundamental diagnostic character. Indeed, generic separation is based largely upon it. It is interesting to note that *Calamodendron* and *Arthroxylon*, with segments composed of prosenchyma flanking primary rays and solid prosenchyma respectively, are specialized. Variation in such segments is so small, even on a theoretical basis, that very few species in these two genera have been described, and it is likely that there will be very few more in the future for this reason. On the other hand, the fact that *Arthropitys* has a large number of species may perhaps be due to the fact that it has an unspecialized segment starting from the pith with a band of homogeneous parenchyma that may vary considerably. Williamson and Scott (1895) outlined the variability of interfascicular segments, which was later refined by Knoell (1935) to include variation of the primary ray in *Arthropitys*. This outline appears as follows.

- 1. Primary ray persists in secondary wood.
 - a. Primary ray remains constant in width.
 - b. Primary ray gradually becomes narrow.
- 2. Primary ray does not persist in secondary wood.
 - c. Primary ray disappears abruptly with onset of cambial activity.
 - d. Primary ray disappears somewhere in secondary wood.
 - (1) Proportion of ray parenchyma in interfascicular wood then becomes equal to that in fascicular wood.
- (2) Proportion of ray parenchyma in interfascicular wood becomes greater than that in fascicular wood.
 Of interest are the several ways by which rays diminish or disappear within secondary wood. They have been summarized in essence by Knoell as follows:

- 1. Tapering due to decrease in cell size or cell row number.
- 2. Tapering due to insertion of new tracheid rows at margin.
- 3. Tapering due to replacement of ray cells by tracheids in flanking rows.
- 4. Disintegration due to insertion of new tracheid rows between median rows.
- 5. Disintegration due to replacement of ray cells by tracheids in median rows. One or more of these factors operate in any species and should be noted in a

description.

Tangential sections show best the vertical extension of primary ray cells, which is of diagnostic value. Also supra- and infra-nodal canals appear in this view as swellings at each end of a ray. When tissue is present, it is irregular, isometric parenchyma. The infra-nodal canal is the larger of the two, making it possible to orient the direction of the axis. In some stem species canals are not prominent, but in others they persist as hollow structures even after the primary ray has disappeared, and are real "canals." The bulk of the collection used in this investigation consisted of some 70 odd stem fragments. Most of them are from three localities: West Mineral, Kansas; Berryville, Illinois; and Booneville, Indiana. A few specimens are from several localities in Iowa, Illinois, and Indiana. Most specimens belong to the genus Arthropitys. There are several specimens of Arthroxylon, chiefly from Iowa, but none of Calamodendron. A few specimens fall into species of European material and a considerable number into American species already described.

ARTHROPITYS illinoensis Anderson, sp. nov.

This species is based on eight specimens collected from Berryville, Nashville, Freeburg, and Dix, Illinois. All stems are decorticated and are of three size classes. Three are hardly more than twigs, with pith diameters ranging from .6 to 1.1 cm. and total diameters from .9 to 1.4 cm. Four are intermediate with pith cavities and total diameters varying from 2.2 to 3.0 cm. and 4.1 to 6.5 cm., respectively. The largest stem is unusual in that its pith (diameter 6.5 cm.) is surrounded by a sheath of secondary wood only .5 cm. thick. It is apparently the remains of a young major axis fossilized before much secondary wood had formed and presumably before the axis had elongated much beyond this level.

Cross-sectional views (pl. 20, fig. 3) show that pith tissue is preserved between fascicular segments only. The segments themselves are wide, spaced nearly 2 mm. apart, and characteristically blunt at the inner edge. Circular protoxylem canals are relatively large, ranging from 175 to 250 μ in diameter. The primary ray disappears quickly, its parenchymatous cells being replaced by tracheids soon after initiation of cambial activity. Fascicular segments merge into a homogeneous sheath of secondary wood interspersed with secondary rays. A tangential section cut fairly near the pith (fig. 7) shows alternate wood sectors and primary rays. Ray cells are elongate vertically and may reach 300 μ in height. Near the nodes rays enlarge at both ends into the nodal canals formed of irregularly packed, isometric cells. Within an internode secondary rays are sparse and hard to see because

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they are uniseriate and composed of elongate cells, $100-300 \mu$ tall, separated by slanting cross walls. Within a nodal region secondary rays are numerous and multi-seriate. Figure 5 is a radial section showing rays cut in various sections. Here the elongation of ray cells is more apparent. Tracheids have three to four rows of alternate bordered pits.

The type specimen is of special interest since there are three roots attached to it which appear to be referable to Astromyelon Williamsonis (Cash and Hick) Williamson. These decorticated roots are about 1.5 cm. across. Broad, blunt, fascicular segments with prominent central secondary rays, large centripetal tracheids, uniform fascicular and interfascicular wood, so characteristic of A. Williamsonis, are easily observed. The segments originate from the innermost wood of the stem and at the same level as leaf traces. The pith cavity enlarges gradually in its outward course, and toward the inside there seem to be peripheral "canals" which are really small groups of large, thin-walled cells, giving the root primordium a stem-like appearance; they disappear farther out. The course of the root is perpendicular to the stem axis for about 1 cm.; then it gradually bends downward at a 30 degree angle upon emerging from the stem stele.

Diagnosis.—Decorticated stem 1–6.5 cm. in diameter, and internodes 1– several cm. long; pith cells usually absent; primary wood scarce, partially bordering a circular protoxylem canal 175–250 μ across; fascicular segment blunt at inner edge, broad and merging with others due to rapid loss of primary ray; tracheids with several rows of alternate oval pits; secondary rays sparse, uniseriate with elongate cells up to 300 μ tall, except at nodes where they are copious, multiseriate,

and short-celled.

Type specimen: Coal ball no. 947, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and localities:

- 1. Coal ball nos. 860e, 948, 949, 950; Berryville, Illinois.
- 2. Coal ball no. 951; Freeburg, Illinois.
- 3. Coal ball no. 952; Nashville, Illinois.
- 4. Coal ball no. 953; Dix, Illinois.

ARTHROPITYS versifoveata Anderson, sp. nov.

Arthropitys sp. B. Andrews, in Ann. Mo. Bot. Gard. 39:189-218. 1952.

Andrews reported briefly on a large Arthropitys stem fragment from West Mineral, Kansas. Its poor preservation prevented a full description, and no specific name was assigned. Since then at least eight additional specimens of this stem have been collected from the Mineral locality, making possible a definite erection of a new species. All the stems are decorticated and probably fragments from a major axis if not the primary axis, for their pith diameters range from 2.5 to 7.5 cm. and total

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diameters from 5 to 9 cm. Internodes vary with stem diameter and range from 1.2 to 3 cm. Of exceptional interest is the smallest stem (no. 956) which projects several centimeters beyond the end of the coal ball imbedding it, showing its nodes and branching habit. Nodes are spaced 1.2 cm. apart and each bears four branches 4 mm. thick and 90 degrees apart. Branches of one node alternate with those of adjacent nodes. That these structures are branches and not roots is proved by a tangential section showing them to arise somewhat above the level of leaf traces, as is characteristic of calamitean branches. It is therefore possible to place this species in the Cruciatus subgroup of the Eucalamites group of impression species. Most of the pith is lost although it persists at the periphery and as pith disc remnants at nodes. Protoxylem canals are circular, varying from 150 to 200 µ across and are surrounded on three sides by primary tracheids (fig. 6). Each fascicular segment enlarges rapidly by insertion of new tracheid rows at the margin; thereafter it broadens very slowly toward the outside. Rather infrequently new rows of tracheids are inserted at the margin or middle of the ray, narrowing it or cutting it into two or more parts. In tangential section primary ray cells are nearly isometric, being elongated toward the margin (fig. 4). Secondary tracheids have either scalariform or reticulate-bordered pitting (figs. 9 and 10). Both types are scattered at random throughout a stele and the proportion of each varies considerably among stems. So, while variation in proportion of pitting type is individual, the presence of this curious mixture is characteristic to this species along with a number of other features that are more constant. Secondary rays are made up of cells up to 200 μ tall. Rays are strictly uniseriate near the pith but may be biseriate farther out. Within nodal regions wood rays become more frequent and thicker. This species is much like A. kansana Andrews with which it is usually found. Smaller primary wood groups, lack of strictly bordered pitting of tracheids or prominent biseriate rays are the chief characters that set it off from A. kansana. Diagnosis.-Decorticated stem 5-9 cm. in diameter with internodes 1.2 to 3 cm. long; branches at every node alternating with those at adjacent nodes; protoxylem canal 150–200 μ across, surrounded on three sides by a relatively large amount of metaxylem; fascicular segment blunt, broadening very slowly and remaining distinct in outer wood; primary ray persisting as a band 4-6 cells wide, occasionally narrowed or split by insertion of new tracheid rows at margin or center; tracheids with scalariform or reticulate bordered pitting, both types scattered irregularly throughout the stem and in different proportions among stems; secondary rays of

cells up to 200 µ high, uniseriate and sparsely biseriate in outer wood. *Type specimen:* coal ball no. 829, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: West Mineral, Kansas; Fleming coal, upper Cherokee shale, Des Moines series; Middle Pennsylvanian. Other specimens and locality: Coal ball nos. 754, 788, 826, 828, 954, 955, 956; West Mineral, Kansas.

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ARTHROPITYS SP.

The following description is based upon a fragmentary specimen (coal ball no. 957) from New Delta, Illinois. Although it appears to be a new species it will not be given a species assignment because of its poor preservation and fragmentary condition. Only a sector of the stele is preserved showing a small part of the pith cavity surrounded by 2 cm. of secondary wood. Protoxylem canals are about 200 μ across and appear to abut directly onto the secondary wood. The fascicular segment is relatively narrow, ranging from .5 to 1.0 mm. passing toward the outermost secondary wood. The primary ray is about six cells wide and persists undiminished in the secondary wood (fig. 12). Secondary rays are uniseriate near the pith but farther out they are multiseriate and may be nearly as large as primary rays, giving the wood a somewhat uniform appearance in tangential view (fig. 8). Tracheids have three or four rows of circular pits on the radial walls. With its uniform primary ray and small pith cavity relative to thickness of secondary wood, this species resembles A. bistriata, but tracheids are pitted instead of scalariform as in this European species.

OTHER STEMS

There are two large stems (nos. 772 and 937) of Arthropitys communis from West Mineral, Kansas, that are very typical, with blunt, narrow fascicular segments, small protoxylem canals, scalariform tracheids and diminishing primary rays. Another specimen (no. 932) of this species is from Atlas Mine near Oskaloosa, Iowa. It is rather badly preserved, and this determination is tentative. From Berryville, Illinois, several more specimens of A. communis var. septata Andrews have been collected (nos. 938-943), all of them remarkably alike, especially with 6-8 mm. internodes and septate tracheids of inner secondary wood. The status of this variety is more certain, because these characters which might seem questionable stand up statistically. Indeed, it can be suggested that this variety deserves specific status. In a coal ball (no. 841) from Booneville, Indiana, there is a calamite stele with 9 cm. of secondary wood. Since only a sector of the stele is preserved, pith diameter is estimated to be 12 cm. From tangential sections it is seen that primary rays split into short, overlapping, multiseriate rays only slightly larger in outer wood than secondary rays, which also become multiseriate in outer wood. In the outermost wood there is a very high proportion of ray tissue and relatively few tracheids. Tracheids have alternate oval pits on their radial walls. By its size and anatomy this specimen is assigned to Arthropitys gigas. Arthropitys Hirmeri Knoell is represented in a coal ball from Pinckneyville, Illinois (no. 568). It is a small stem with little secondary wood and has the characteristically abrupt loss of the primary rays immediately upon initiation of secondary growth. From West Mineral, Kansas, there are six stems identified as Arthropitys kansana (nos. 750, 787, 789, 791, 830, 944). Also most stems (nos. 837, 838, 839, 840,

844, 877, 945) from Booneville, Indiana, are undoubtedly A. kansana despite the fact that their aspect is slightly different from the Kansas specimens. Upon careful comparison it is found that every character of the Booneville stems matches that of the West Mineral stems: general size, orientation of primary wood with pith and fascicular segments, protoxylem canal size of 250 μ , very slow diminution of the primary ray which is made up of small isometric cells, presence of biseriate rays in secondary wood, and several rows of alternate bordered pits on radial walls of tracheids. Their slightly different aspect is interpreted as an outcome of general difference in preservation of material between the two localities.

There is one Booneville specimen (no. 875) very similar to A. kansana, but it has scalariform pits on tracheids and ray cells tend to be elongated. The primary ray does not appear to diminish in the small amount of secondary wood present. This stem is tentatively assigned to A. bistriata.

Arthroxylon Williamsonii Reed is represented by three small stems, one (no. B-13) from Oskaloosa, Iowa, and the other two (nos. 933 and 936) from What Cheer, Iowa. A fourth stem (no. 946) comes from West Mineral, Kansas, and is unlike all stems previously described because of its large size. Pith diameter is 7.3 cm. and secondary wood is 2.3 cm. thick. It is identical with the Arthroxylon stem briefly reported by Andrews (1952). Like most West Mineral calamites it is fusainized from the pith cavity outward and highly pyritized from the outside in. Between pyritized and fusainized zones there is a small neutral band, the only hope for good study, suggesting that factors promoting formation of the two conditions are opposing and each tends to prevent the other from occurring. Primary wood and protoxylem canals can be seen, however, and are like those of A. Williamsonii; this specimen is probably a primary axis of this species. A tangential section through the well-preserved zone, cut about 1 cm. from the pith (fig. 13), shows that the fibrous zone does not contrast as sharply with the fascicular segment as in smaller stems. Another difference is the presence of a larger proportion of short-celled secondary rays, even in the fibrous zone, where they are absent in smaller stems. Such increase of ray parenchyma is probably in accordance with Bower's "size and form" principle and does not represent specific difference.

TWIGS AND LEAVES

Calamitean twigs are seldom found in coal balls although they are found as impressions in abundance. Williamson described some petrified twigs, and Hick (1894) gave a full treatment of them, noting their very close similarity to stems of *Equisetum*. Andrews (1952) briefly described two twig specimens probably identical to those described below. Isolated leaves are also infrequently found. Hick (1895) wrote a short account of them, but a more comprehensive treatment was made by Thomas (1911) who brought together scattered information about leaves and designated several specific types. In America only Hoskins (1928) and Reed (1938) have described petrified calamitean leaves.

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In the present study the smallest stems found range from .7 to 3.0 mm. in diameter, forming a size class distinct from another class which ranges from 6 to 10 mm. The smaller class will be termed twigs in this paper, and the larger small stems. Only the twigs are definitely assigned to the new species erected below.

CALAMITES rectangularis Anderson, sp. nov.

This species is based on a large assemblage of shoots, isolated twigs and leaves in three coal balls from Berryville, Illinois.

In considering twig size, the diameter of the primary body (including distance across the pith plus primary wood) is more informative than total twig diameter.

Since the cortex is somewhat uniform in thickness, complications of including secondary wood are thereby avoided and errors in measurement due to loss of phloem in preservation are minimized. Also, the distinction between twigs and stems is more apparent when the diameter of the primary body is used rather than total stem diameters. The primary bodies of 58 twigs measured varied from .2 to 1.0 mm. in diameter, with a median and mode of .6 mm. This variation shows a normal distribution; hence these twigs represent the highest order or ultimate branches of a calamite. The measurements show that these coal balls happened to preserve an ultimate branch system that is often preserved intact in an impression. For comparison, an impression of *Asterophyllites charaeformis* Sterenberg, taken at random, shows the last three degrees of branching. The largest axis is fragmentary and measures 4 mm. in diameter. The secondary axes are 1.5 mm. across at the base and .5 mm. near the tip, and the ultimate axes are .2 to .4 mm. across. The smallest

part of the secondary axis is about as large as the largest ultimate branches, so it is possible that the fragments in the coal balls may represent two degrees of branching instead of one.

Leaves measure .3-.5 mm. in thickness, .5-.7 mm. in width, and 5-10 mm. in length. Thirteen leaves per whorl may be counted in one specimen (fig. 14), and other shoots appear to have about 12 per whorl. Variation in leaf size seems to be comparable to that in twig size. Figure 16 shows a representative longisectional view of a shoot.

The anatomy of a twig is typically calamitean, with a ring of fascicular segments, each with a protoxylem canal, unpreserved phloem, and primary cortex of two layers. The smallest twig is .6 mm. in diameter with a primary body .2 mm. thick. There are five fascicular segments and no secondary wood. A betterpreserved specimen, shown in fig. 20, is slightly larger and 1 mm. in diameter; the primary body is .4 mm. thick, and has seven fascicular segments. The cortex is intact and there appear to be about twelve leaves per whorl. Twigs with a primary body approaching 1 mm. in diameter have 12 to 20 fascicular segments and may have up to .2 mm. of secondary wood (fig. 19). Otherwise they are quite similar to the smallest twigs. As stated above, leaves seem to vary with their twigs in size. However, the larger leaves form a distinct class, sometimes being $1.5 \times .8$ mm. in cross-section

but found closely associated with small stems about 6 mm. in diameter. Figure 15 shows cross-sections of leaves of both size classes that happen to be adjacent. The larger leaf is $1.5 \times .6$ mm. and the smaller is $.7 \times .4$ mm. They are oriented in the same direction. Their cross-sectional shape is almost perfectly rectangular, quite unlike that of leaves previously described. There is a single layer of epidermis present, with some poorly defined stomata on the lower surface of the larger leaf. A palisade layer next underlies the surface and extends nearly around the central tissues. At the center there is a single strand of perhaps 20 tracheids. Phloem cells are probably not preserved. Surrounding the stele is the bundle sheath, which is proportionally larger than that in other species. Next to the stele, cells of the sheath are large and very thin-walled. Toward the outside they are smaller with thicker walls, and in longisectional view they appear fibrous. This fibrous zone is more pronounced on the upper side where it seems to form a sort of backbone for the leaf.

Diagnosis.—Shoot .7-3.0 mm. in diameter, bearing 12 leaves in whorls 1-5 mm. apart; axis calamitean with ring of fascicular segments each with a protoxylem canal and 2-layered cortex; leaves 5-10 mm. long and .3 \times .5 to .8 \times 1.5 mm. and of rectangular shape in cross-section, palisade layer and large bundle sheath surrounding single, unbranched vascular strand.

Type specimen: Coal ball no. 834, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and locality: Coal ball nos. 860, 879, 960; Berryville, Illinois. The larger stem-size class ranges from 6 to 10 mm. in total width. Apart from being larger than twigs their organization is different. Primary wood groups and protoxylem canals are larger and more spaced out. Secondary wood is always present. Figure 18 shows a small stem about 6 mm. thick. There are 24 fascicular segments and .1 mm. of secondary wood. It seems evident, from comparing this stem with twigs one-fourth as large but with about the same number of fascicular segments, that the two represent different orders of branching. It is inconceivable that a twig could expand its width fourfold to become a small stem such as is figured. From this specimen and others scattered throughout the coal balls there can be seen a stelar organization similar to that of Artbropitys illinoensis. Configuration of the primary body and quick loss of the primary ray are partial evidence that the specimens belong to this species. It is further suggested that the twigs and hence the stelar organization is species. It is further suggested that the twigs

and leaves described above also belong to this stem species because of their close association with these small stems.

ROOTS

Petrified calamitean roots were first described in 1878 by Williamson, who assigned them the generic name Astromyelon. He found isolated fragments only and suspected that they might be stems somewhat allied to calamites. It remained

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for Renault and Zeiller (1890) to find them in organic connection with calamitean stems, confirming Renault's earlier hypothesis that they were roots of calamites. Renault also designated four of the five species of Astromyelon so far described. Anatomical descriptions were given by Renault, and by Williamson and Scott (1895a). Maslen (1905) wrote a masterly discussion of root-stem relationships. During the present investigation isolated roots of various size were found, ranging from 2 mm. to several cm. in diameter. Although at least three size classes are represented, no very small roots have been observed of the type formerly called Myriophylloides with diarch or tetrarch protosteles and cortex with large intercellular spaces. In fact, no extra-xylary tissues were preserved in any roots observed. This assemblage appears rather varied anatomically, but some instances of branching make it possible to designate a small number of types. Coal balls (nos. 840, 870, 872, 878, 947, 958) from Booneville and St. Wendells, Indiana, and Berryville, Illinois, were found to contain calamitean roots belonging to Astromyelon Williamsonis. The somewhat indistinct fascicular segments projecting only a little into the pith, quick replacement of interfascicular parenchyma by tracheids, a prominent secondary ray in the middle of each fascicular segment, and very large, thin-walled centripetal tracheids are characters that check point for point with described and illustrated specimens of this species from European coal balls. Such distinct characters are present only in root steles ranging from 4 to 10 mm. in diameter, roots of an intermediate order of branching. Associated steles of smaller size appear somewhat nondescript and similar to roots of this size belonging to other species.

ASTROMYELON cauloides Anderson, sp. nov.

This species is based on a number of roots found in coal balls from Berryville, Illinois, and St. Wendells, Indiana. All specimens are decorticated and their steles range from 2 mm. to several cm. in diameter, with a common anatomical configuration in all sizes except the very smallest which are nondescript.

The most characteristic features of this species in cross-sectional view are the rather pointed fascicular wedges accentuated by the presence of considerable interfascicular parenchyma. In a segment, centripetal metaxylem is reasonably welldeveloped and projects into the nearly intact pith, giving a distinct point to a segment. Wood rays are mostly uniseriate. The primary ray is lost through replacement of parenchymatous cells by tracheids in a radial row of cells plus the insertion of new rows of tracheids. There is considerable variation in the rate of ray loss; smaller roots and some larger ones lose their primary rays almost as soon as production of secondary wood begins (fig. 17), while in others the ray persists through 4 mm. of secondary wood (fig. 1). The writer does not believe that such variation constitutes specific difference, since all other characters are constant, especially the manner of ray loss, and there is a continuous series of ray-loss rates among the observed specimens.

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This root most closely resembles Astromyelon augustodunense Renault, in which the primary ray persists considerably into secondary wood. In this species, however, ray loss is accomplished by a decrease in ray row number only. There is no replacement of parenchymatous cells by tracheids, and the outer tracheidal row of a fascicular segment flanking a ray in the inner wood remains as the flanking row until it meets, in outer secondary wood, a flanking tracheidal row of the next segment. Figure 2 is a tangential section near the pith showing primary rays and wood sectors. Cells of primary rays are large and somewhat elongate $(75-300 \mu)$, as well as those in the uniseriate secondary rays scattered among tracheids. Pitting

on radial walls of tracheids is strictly scalariform.

In its anatomical organization this root appears more like a stem than the other root species. It is further suggested that it belongs to Arthropitys communis var. septata on the basis of association in coal balls and such anatomical details as elongate ray cells and scalriform pitting.

Diagnosis.—Decorticated root 2-40 mm. in diameter; pith nearly intact and of thin-walled parenchyma; primary xylem mesarch with protoxylem poles at periphery of pith, no protoxylem canals present; secondary fascicular wood with scalariform tracheids and 1-2 seriate rays 2 to many cells deep; ray cells up to 300 μ deep; interfascicular segment with a varying amount of primary ray lost through replacement of parenchymatous cells by tracheids in a given row plus insertion of new tracheid rows.

Type specimen: Coal ball no. 853, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and localities:

1. Coal ball nos. 882, 887, 929, 930, 931; Berryville, Illinois.

2. Coal ball nos. 925, 926, 927; St. Wendells, Indiana.

ASTROMYELON pluriradiatum Anderson, sp. nov.

This species is based upon a single specimen in a coal ball from Berryville, Illinois. It most closely resembles Astromyelon reticulatum Renault, which is figured showing very broad fascicular segments similar to those in this new root. However, the small amount of secondary wood in Renault's specimen makes precise comparison impossible. The stele is decorticated, the pith cavity is 6 mm. in diameter, and there are 7 mm. of secondary wood. Figure 21 shows a cross-section that happens to cut a branch root in its outward course; outside the main axis it has a diameter of 1 cm. and organization similar to that of the parent root. The chief characteristic of this root is its high proportion of ray tissue in secondary wood. This is apparent even in cross-section where a very prominent 3- to 4-seriate ray appears centrally in each fascicular segment. In tangential view the high proportion of ray parenchyma (fig. 11) makes the wood appear almost herbaceous. Rays are 1- to 4-seriate and the largest may be over 1 cm. deep.

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Multi-seriate rays form an overlapping network of parenchymatous tissue in the center of a fascicular segment, a condition opposite to that in calamitean stems and most roots where the interfascicular segment is more parenchymatous. Ray cells are little elongated, being rather isometric in multiseriate rays; their depth ranges from 50 to 150 μ .

The pith cavity is nearly hollow with tissue only at the periphery. Fascicular segments are very broad and blunt due to a small amount of primary wood, immediate succession of secondary growth, and rapid insertion of new tracheidal rows in each segment. A radial section through a protoxylem pole shows annular

tracheids of protoxylem and a few scalariform tracheids of centrifugal metaxylem. Cells of the centripetal xylem are pitted and seem to be transitional to parenchyma, for they are shorter, have thinner walls and squared end-walls. Secondary tracheids have either single rows of elongate pits or 3-4 rows of alternating oval pits and are up to 50 \times 60 μ in cross-section. Primary rays lose their identity quickly through rapid tapering and replacement of parenchymatous cells by tracheids in any given cell row.

Diagnosis.—Decorticated root 2 cm. in diameter with connected branch root 1 cm. thick; pith 6 mm. across, hollow, with peripheral parenchyma only; primary xylem mesarch with 12 protoxylem poles at periphery of pith; centripetal metaxylem of thin-walled, short, square-ended tracheids; fascicular segments very broad and blunt facing the pith; secondary wood with high proportion of ray parenchyma, especially in center of fascicular segment where there are up to 4-seriate rays; ray cells 50–150 μ deep; secondary tracheids to 50 \times 60 μ in cross-section with single rows of elongate pits or several rows of alternate oval pits; primary ray lost through replacement of parenchymatous cells by tracheids in a given radial row of cells. *Type specimen:* Coal ball no. 959, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

CONES

In the thirty-odd years in which coal balls have been cut and studied in America, calamitean cones have very rarely been discovered in them. Some of the earlier workers listed their occasional presence, but to date there have been no descriptions of them, although several paleobotanists are currently working on such cones and papers should be soon forthcoming. The present investigation covers nine cone specimens, eight of which belong to one species. All of them are assignable to *Palaeostachya* owing to adaxial insertion of sporangiophores. One of the cones is about 2 cm. in diameter while another is at least 3 cm. in diameter. None of the *Palaeostachya* species described from petrifactions comes close to approaching this size, and, of impression species, only *P. arborescens* Sternberg and *P. Schimperiana* Weiss are in this size class, being 3 and 2.5 cm. in diameter respectively (Weiss,

1876, 1884). Correlation of these impression species with the new petrified cones is ruled out, since *P. arborescens* has about 20 bracts per whorl while the corresponding petrified cone has from 40 to 60; and *P. Schimperiana* has an axis 1 cm. thick while the petrified cone has one about 4 mm. thick.

PALAEOSTACHYA multifolia (Reed) Anderson, comb. nov.

Calamites multifolia Reed, in Bot. Gaz. 100:324-335. 1938.

This species is based upon six specimens in coal balls from Berryville, Illinois, and two in a single coal ball from Booneville, Indiana. The complete cone is at least 8 cm. long and 3 cm. wide. Toward the base it narrows to 1.5 cm., the tapered zone being sterile. Nodes are spaced 3 to 4 mm. apart and bear 40-60 whorled leaves fused at their bases. Sporangiophores arise obliquely from bract axils and bear four pendant sporangia. This species is heterosporous.

At the very base the axis is small and consists of xylem only. The primary body is 2 mm. in diameter and secondary wood is .5 mm. thick making the total diameter 3 mm. In cross-section it is perhaps indistinguishable from a stele of a vegetative twig (fig. 22). A few scattered bracts are present at this level. The stele then enlarges to its full width of 6 mm. in a distance of 2 cm. A cross-sectional view of the widened axis shows a somewhat different organization than that below. The stele is crushed to an elliptical shape, and loosely surrounding cortex is present. There are now 26 fascicular segments in contrast to 18 at the level below. Segments show a tendency to group into pairs and there are .3 mm. of secondary wood. The uppermost cross-section of the axis shows it to be the same size, but with very little secondary wood, and a very pronounced tendency for the segments to group in pairs (fig. 24). There are now 30 fascicular segments. Since there is very little secondary wood at this level, the cone probably does not extend much farther. A tangential section through the stele gives proof that bracts of one whorl are superposed on those of the whorl below. At most nodes fascicular segments of the internodes above and below stand directly in line with each other. Only a few show alternation at nodes, marking the insertion of new segments into the stele. Hence, most leaf traces and their bracts arise directly above each other.

The bracts of a whorl number from 40 to 60 in the widest part of the cone and are fused basally into a lateral disc. This disc is very well shown in the specimen from coal ball no. 858 (fig. 25). When a small piece of the cone was accidentally broken off, the top surface of a whorl of fused bracts was exposed. One-fourth of the whorl contains 10 bracts, so the whorl must contain 40. This whorl is near the base of the cone and does not have the maximum number of bracts possible. From the photograph it can be seen that the bracts are fused into a basin-like disc, with the mid-portion of each bract ridged somewhat. The disc dips down a little before bending up sharply to a rim where the bracts separate. Cells composing the disc are rather elongate with walls of moderate thickness. This tissue persists into the upturned free bract, forming a sort of "backbone" which gradually disappears. At the rim of the disc on its lower surface the lamina of each bract projects

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abruptly, extending down as much as 3 mm., where it practically touches the disc below nearly enclosing the sporangia (fig. 23). Any cross-section cuts the free bract tips at several levels since the tips overlap four nodes above before terminating (fig. 24). Innermost is the disc cut on the bias; next the upturned disc is still fused but with the lamina of each bract added; the next outer whorl shows free bracts without disc tissue; and the outermost whorl shows a small, nondescript bract tip. There is some sort of imbricate pattern of the bracts, but since they are superposed, the pattern must be due to local displacement of free tips. Sporangiophores arise in bract axils, traverse an oblique course upwards (fig. 26), flatten out and bear 4 sporangia (fig. 27). Figure 24 is a cross-section of the cone on a 30-degree slope, which shows sporangia from a somewhat tangential view. The number of radial rows of sporangia approximately equals the number of bracts, and there is one sporangiophore for every two radial rows of sporangia. Thus it is inferred that the number of sporangiophores is one-half that of the number of bracts. At this level the axis has 30 fascicular segments, each of which presumably gives off one sporangiophore as in other Palaeostachya species described by Renault (1882) and Hickling (1907). Hence, there must be about 60 bracts per whorl at this level, which cuts through this cone at its full width. Whether sporangiophores alternate or are superposed on bracts cannot be determined. Sporangia fill most of the space between whorls of bracts and must have been $5 \times 2 \times 2$ mm. in size. The wall is made of a single layer of cells which are somewhat elongated in surface view.

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This species is heterosporous. Microspores and megaspores have spherical shape; their walls are thin, psilate and tend to fold; and the triradiate mark is small—all of these characters placing them in the genus *Calamospora* Schopf, Wilson & Bentall (1944). In coal ball no. 839 only microspores are found, which measure from 60 to 80 μ in diameter. The type cone in coal ball no. 860 has microspores of the same size (fig. 28), and in one spot near the tip are some scattered megaspores 180 μ in diameter (fig. 29). In the cones from coal balls nos. 882 and 858 only megaspores are present (fig. 30), and they are badly shattered so that isolation is impossible. These megaspores vary from 250 to 280 μ in diameter. In no. 882 are associated structures that may be microspores, but owing to poor preservation it is not possible to observe definite spore characters.

As Hartung (1933) has pointed out, heterospory in the calamites is rather frequent. Indeed, this family shows more incipient heterospory than any other in the plant kingdom in terms of relative frequency and the fact that microspores and megaspores never differ as much in size as do those in other heterosporous groups. Considering such observed frequency, it is puzzling that the calamites did not reach the "seed" habit as did the lepidodendroids. Apparently *Palaeostachya multifolia* was a species in a transition to heterospory, for the only specimen giving positive evidence of heterospory in the same cone has megaspores considerably smaller than those in cones containing megaspores only, assuming that the latter are true megasporangiate cones having reached the limit of heterospory observed in the calamites.

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Coal ball no. 961 contains a cone that is notable because its developing apex is preserved. The length of the whole shoot is about 10 cm. Organization of the axis and bracts places it clearly within this species even though there is no trace of any sporangia. There are some associated structures that might be spores, but they do not possess definite spore characters. This specimen checks point for point with *Calamites multifolia* Reed, and since it is a developing shoot, as is Reed's, its identity is evident. Total size, presence of forty leaves per whorl fused basally into a disc, bract size, shape, and organization are features in common. There is also grouping of fascicular segments into pairs, which Reed noted as a feature of *Palaeostachya*

vera Seward. Therefore, it seems apparent that Reed's twig is a developing cone in which sporangia were not yet developed or destroyed in fossilization.

The meristem itself is worthy of note since so few are known in paleobotany. The first peel to show the shoot apex reveals no less than 11 surrounding whorls of leaves in various developmental stages (fig. 31). Cells of the apex are isometric, about 30 μ in diameter, and show a tendency to periclinal division toward the shoot margin. Immediately below this region the tissue appears to be crushed from one side; but 1 mm. below the apex this distortion disappears, the shoot has nearly reached full width, a hollow pith cavity has formed, and even vascular tissue has begun to differentiate. Such a blunt apex is very similar to that of Equisetum. Further development shows that once primary xylem is formed, its position or distance from the shoot center does not change with the addition of secondary wood. A problem arises in accounting for the difference between the number of fascicular segments and the number of bracts at a given node. In this species there are about 30 segments and 40 bracts per whorl. In calamites there is usually one leaf trace given off per segment, but favorable sections of this cone show three traces developing from some pairs of fascicular segments. In this way an appropriate increase in leaf trace and bract number occurs.

Since all the specimens are shattered or fragmentary, a drawing is appended to give a better visual impression of the morphology and proportions of this cone (text-fig. 1).

Diagnosis.—Cone 8 cm. long and 3 cm. wide, tapering to 1.5 cm. near the base; axis 1 cm. wide with hollow pith cavity, 30 fascicular segments grouped in pairs, each with protoxylem canal and secondary wood; bracts 40-60, whorled at nodes and fused into a lateral disc around the axis, and with tips upturned, free and 1.5 cm. long; sporangiophores 30 at node, inserted at level of upper bract surface, and bearing 4 pendant sporangia; heterosporous with microspores 60-80 μ and

megaspores 190 to 280 µ in diameter; spores of genus Calamospora. Type specimen: Coal ball no. 860, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

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Text-fig. 1. Longitudinal reconstruction of Palaeostachya multifolia based upon specimen in coal ball no. 860, \times 2.

Other specimens and localities:

- 1. Coal ball nos. 834, 843, 858, 961; Berryville, Illinois.
- 2. Coal ball no. 839; Booneville, Indiana.

PALAEOSTACHYA SP.

The following description is based upon a single specimen in a coal ball from What Cheer, Iowa. Its structures are obscured considerably by pyrite, and most tissue appears partly decomposed. Strangely, cortical tissues are present while most of the tracheids have disappeared. The cone is 5 cm. long and 2 cm. wide. Its axis is 5 mm. in diameter, rather slender for a cone as large as this, and is set with

whorls of 24 bracts spaced 4.5 mm. apart. In three nodes studied, 14 sporangiophores arise somewhat above and between the bracts. One sporangiophore presumably develops from one fascicular segment of the main axis and terminates in a fleshy, cruciate structure bearing 4 sporangia. Sporangia contain microspores 75-100 µ in diameter belonging to the genus Calamospora.

A point of interest is the relationship between number of bracts and of sporangiophores at a node. In this specimen 24 bracts and 14 sporangiophores are counted at each node. Also sporangiophores seem to come off the axis in pairs, probably a consequence of their parent segments in the main axis being grouped in pairs. In several observed instances each sporangiophore of a "pair" is placed on each side of a given bract. This further complicates the picture so that no possible symmetrical arrangement of 24 bracts and 14 sporangiophores at a node can be devised. It follows that no exact relationship exists between bract and sporangiophore number; thus tending to support Hickling's (1907) theory that sporangiophores belong to a separate node that moved downward phyletically to coincide with the bracteate node. It was also observed that sporangiophore number is controlled by fascicular segment number (one segment gives off one sporangiophore) while bract number is not rigidly controlled by segment number, as demonstrated in P. multifolia, thus accounting for the independence of bract and sporangiophore number.

STRATIGRAPHIC CORRELATIONS

While there have been stratigraphic correlations of plant impression fossils, made chiefly in Europe, very little work has been done with petrified plant remains found in coal balls. Schopf (1941) compared horizons of various American coal ball localities with each other and with European coal ball horizons as a background for his stratigraphic discussion of Mazocarpon. To date no general stratigraphic correlation of megafossil species has been prepared which would supplement spore studies in solving stratigraphic and floristic problems of past ages. If the paleobotanists studying coal balls could cooperate in a publication giving the results of their researches, a general picture of vertical and horizontal distribution of megafossil species might be obtained. The following is a very meagre contribution toward this end, involving only petrified calamitean species described in this investigation and those reported by Andrews (1952).

Calamitean remains were recovered from the following coal ball localities, all of which occur in Middle or Upper Pennsylvanian deposits.

1. What Cheer, Iowa; Des Moines series.

- 2. Atlas Mine, near Oskaloosa, Iowa; Des Moines series.
- 3. Argus Mine, near Oskaloosa, Iowa; Des Moines series.
- 4. West Mineral, Kansas; Fleming coal, Cherokee shale, Des Moines series.
- 5. Red Ray Mine, Freeburg, Illinois; No. 6 coal, Carbondale group.
- 6. Pyramid Mine, Pinckneyville, Illinois; No. 6 coal, Carbondale group.
- 7. New Delta, Illinois; No. 6 coal, Carbondale group.

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8. Nashville, Illinois; No. 6 coal, Carbondale group. 9. Dix, Illinois; Calhoun coal, McLeansboro group. 10. Berryville, Illinois; Calhoun coal, McLeansboro group. 11. Booneville, Indiana; Petersburg coal No. 5, Petersburg series. 12. St. Wendells, Indiana; near Parker coal, Conemaugh series. Species and their localities are listed below: Arthropitys communis: West Mineral, Berryville and Atlas Mine. This species has a considerable vertical distribution comparable to that in Europe. Arthropitys communis var. septata: Berryville.

Arthropitys gigas: Booneville. This horizon is considerably below that of European horizons, uppermost Carboniferous and lowermost Permian, from which this species has been reported.

Arthropitys bistriata: Booneville. Conditions here as with A. gigas. Arthropitys Hirmeri: Pinckneyville. This horizon is somewhat above the Katharina deposits of the Ruhr from which this species was first reported.

Arthroxylon Williamsonii: What Cheer, Argus Mine, and West Mineral. These localities are probably near the same level and above the Lower Coal Measures of England from which this species was reported earlier.

Astromyelon Williamsonis: Berryville and St. Wendells. These localities are near the same level and much higher than the Lower Coal Measures of England from which this species was first reported. Astromyelon cauloides: Berryville and St. Wendells. Astromyelon pluriradiatum: Berryville.

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Arthropitys illinoensis: Berryville, Red Ray, Dix and Nashville. This species appears to have a reasonably wide vertical distribution but so far is confined to central Illinois.

Arthropitys versifoveata: West Mineral.

Arthropitys kansana: West Mineral and Booneville. Booneville is somewhat above West Mineral stratigraphically and several hundred miles away, giving this species a wide distribution.

Calamites rectangularis: Berryville.

Palaeostachya multifolia: Berryville, Booneville and Harrisburg, Indiana (Reed). This cone species has some vertical distribution, and the Booneville locality is at the same level as Harrisburg, from which Reed recovered a vegetative base of this cone.

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EXPLANATION OF PLATE 20

Figs. 1 and 2. Astromyelon cauloides Anderson: Fig. 1. Cross-section of portion of large root. Coal ball no. 853. Peel 853. X 14; fig. 2. Tangential section of wood near pith showing wood sector and primary rays. Coal ball no. 853. Slide 2360. X 28.

Fig. 3. Arthropitys illinoensis Anderson. Cross-section of inner wood portion. Coal ball no. 947. Peel 947. X 12.

Fig. 4. Arthropitys versifoveata Anderson. Tangential section of wood showing wood sector and primary rays. Coal ball no. 829. Slide 2356. X 31.

Fig. 5. Arthropitys illinoensis. Radial section of wood showing secondary ray cells and tracheids. Coal ball no. 947. Slide 2358. X 75.

Fig. 6. Arthropitys versifoveata. Cross-section of inner wood portion. Coal ball no. 829. Peel 829. X14.

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PLATE 20





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PLATE 21



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EXPLANATION OF PLATE 21

Fig. 7. Arthropitys illinoensis Anderson. Tangential section of wood near the pith showing wood sector and primary rays. Coal ball no. 947. Slide 2357. X 28.

Fig. 8. Arthropitys sp. Tangential section of outer wood showing tracheids, primary rays and a large secondary ray. Coal ball no. 957. Slide 2359. X 33.

Figs. 9 and 10. Arthropitys versifoveata Anderson. Pitting in radial walls of tracheids. Coal ball no. 753. Slide 1924. X 133.

Fig. 11. Astromyelon pluriradiatum Anderson. Tangential section of wood. Coal ball no. 959. Slide 2363. X 28.

Fig. 12. Arthropitys sp. Cross-section of wood portion showing sectors and undiminishing primary rays. Coal ball no. 957. Peel 957. X 11.

Fig. 13. Arthroxylon Williamsonii Reed. Tangential section of wood showing shortcelled secondary rays in woody and fibrous zones. Coal ball no. 946. Slide 2354. X 16.



EXPLANATION OF PLATE 22

Calamites rectangularis Anderson (except fig. 17)

Fig. 14. Nodal cross-section near apex of shoot showing departure of whorled leaves. Coal ball no. 834. Slide 2366. \times 42.

Fig. 15. Cross-sections of leaves. Coal ball no. 860. Slide 2368. \times 39. Fig. 16. Longisection of shoot. Coal ball no. 879. Peel 879A-tan 11. \times 6.

Fig. 17. Astromyelon cauloides Anderson. Cross-section of small root. Coal ball no. 882. Peel 882A. \times 7.

Fig. 18. Cross-section of small stem. Coal ball no. 860. Peel 860J-t1. \times 11. Fig. 19. Cross-section of large twig. Coal ball no. 860. Slide 2367. \times 21. Fig. 20. 'Cross-section of small twig. Coal ball no. 960. Slide 2364. \times 44.

